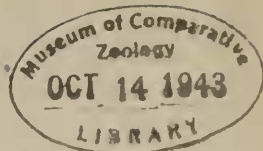


SUBSTITUTE FOOD-PLANTS.

(With a Table of Preference-Groups.)

By E. P. WILTSHIRE, F.R.E.S.

13,820



Previous contributions to the *Entomologist's Record* under this title have appeared in 1942 (Vol. liv) on pp. 63, 107, 122, and 1943 (Vol. lv) on p. 1. It appears, however, desirable, at this point in this interesting discussion, to review the phenomenon, from the systematic and ecological point of view, more broadly, first deciding what is the point at issue. The drawing of conclusions from the completed review will not mean, however, that the last word will thereby have been said.

The subject of these discussions has been consistently described as "substitute food-plants"; but some disagreement has arisen in explaining the phenomenon referred to by this rather ambiguous expression. In answer to the implied question: "Why do larvae have substitute food-plants?" two explanations have been offered: (a) "The common associated evolution of insect and plant"; (b) "Chemotropism is involved: probably all the species of plant within a family (not merely a genus) have a scent which contains a common element."

The propounder of the second of these explanations has also introduced the theory of the existence of intra-specific races or strains preferring one or another of the alternative food-plants. This makes it clear that he is more interested in the question: "Why do individual larvae of a species prefer one or another of the alternative food-plants of its species?" than in the question: "Why do the larvae of a species prefer a certain group of food-plants to the exclusion of other food-plants?" on which the theory of specializing strains has no bearing. If debaters are trying to answer different questions, disagreement in their replies is not to be wondered at.

To avoid any further confusion, therefore, it must at the outset be stated that the problem here discussed is, when formulated as a question: "Why do non-polyphagous larvae prefer certain groups of food-plants to the exclusion of others?" and that the recorded food-plants of the species as a whole over its entire range are under consideration rather than the observed food-plants of an individual larva or strain in one locality.

Our subject thus defined, there need be no further place in this article for the irrelevant theory of intra-specific specializing strains referred to above, except to remark that it incidentally provides an attractive hypothesis of the way in which a new species might evolve, e.g., *Cucullia scrophulariae*, Cap., evolving from the ancestor of *Cucullia verbasci*, L., owing to a racial specialization, in one habitat, on *scrophularia*. (If the records of *scrophulariae* feeding occasionally on *verbas-cum* are correct, this would be a not unnatural reversion to ancestral type, perhaps due to stress of circumstances.)

While there are polyphagous larvae at one end of the scale and strictly monophagous larvae at the other, our present review is only concerned with an intermediate class of larva closer to monophagy than polyphagy, for which the term "oligophagous" may be coined. We can exclude from this review the polyphagous larvae because they show comparatively little preference, and a tabulation of their recorded food-plants would require a life-time's research and a volume of close print;

and we can also exclude the strictly monophagous larvae, because there is no question, in their case, of any "substitute food-plant." It will, however, later appear that the excluded monophagous larvae shed no little collateral light on our subject. It is doubtful whether a satisfactory boundary-line can be drawn between polyphagous and other larvae, for there seem to be all degrees of transition to polyphagy; nevertheless, for the present purpose it is necessary to select an oligophagous class of larvae, although in other contexts this selection may have little reason for existence.

This selection has been made from the British Macro-Lepidoptera list, plus some other Palaearctic Lepidoptera with which I have become acquainted in the Middle East. Most of this multitude of species fails to qualify as oligophagous. For the determination of their food-plants, reference has been made to South, Blaschke, and my own records.

If we now tabulate the food-plants of these larvae, we find that they fall into well-defined groups of plant-genera. These groups, moreover, in most cases correspond with systematic groups.

TABLE OF GROUPS OF FOOD-PLANT GENERA PREFERRED* BY OLIGOPHAGOUS LARVAE.

A. GROUPS CORRESPONDING WITH BOTANICAL SYSTEMATIC AFFINITIES.

I. PRUNUS GROUP.

ROSACEAE : 1, *Prunus*; 2, *Amygdalus*; 3, *Pyrus*; 4, *Crataegus*.

Eriogaster amygdali, Wilt., 1, 2, 4; *Cilix glaucata*, 1, 4; *Diloba caeruleocephala*, 1, 2, 3, 4; *Meganephria oxyacanthae*, 1, 4; *Meganephria renalis*, Wilt., 1, 2, 4; *Epitherina rhodopoleos*, Wehrli, 1, 2, 4; *Nychiodes* genus, 1, 2, 4.

II. BETULA GROUP.

BETULACEAE : 5, *Betula*; 6, *Alnus*; 7, *Corylus*.

Notodonta dromedarius, 5, 6, 7.

III. POPULUS GROUP.

SALICACEAE : 8, *Populus*; 9, *Salix*.

Dicranura vinula; *Cerura syra*; *Pygaera pigra*; *Marumba populi*; *Eusphecia pimptaeformis*, Ob.; *Trochilium crabroniformis*; *Catocala nupta*, *elocata*, *puerpera* and *lesbia*; all on 8 and 9.

IV. PISTACCIA GROUP.

ANACARDIACEAE : 10, *Rhus*; 11, *Pistaccta*.

Anua tirhaca; *Eutelia adulatorix*; both on 10 and 11.

V. NERIUM GROUP.

APOCYNACEAE : 12, *Vinca*; 13, *Nerium*.

Deilephila nerii, 12, 13.

VI. VERBASCUM GROUP.

SCROPHULARIACEAE : 14, *Verbascum*; 15, *Scrophularia*.

Melitaea trivia; *Cucullia verbasci*; both on 14 and 15.

VII. GENISTA GROUP.

PAPILIONACEAE : 16, *Cytisus*; 17, *Genista*; 18, *Spartium*; 19, *Ulex*; 20, *Sarothamnus*; 21, *Glycyrrhiza*; 22, Other *Papilionaceae*; 23, *Laburnum*.

Many *Lycaenidae* on 22; *Apopestes spectrum*, 18, 21; *Dasycorsa modesta* 18, 22; *Pseudoterpna pruinata*, 16, 17, 19, 23; *Fidonia limbaria*, 16, 17, 20; *Chesias spartiata*, 16, 20; *Chesias rufata*, 16, 17, 20.

VIII. SOLANUM GROUP.

SOLANACEAE : 24, *Solanum*; 25, *Lycium*; 26, *Datura*.

Acherontia atropos, 24, 25, 26; also recorded as eating 72.

*"Preferred" here means "Chosen to the exclusion of other plants."

IX. *PINUS* GROUP.

PINACEAE: 27, *Pinus*; 28, *Cedrus*; 29, *Abies*.

Sphinx pinastri, 27, 28; *Dendrolimus pini*, 27, 28, 29; *Thera variata* (= *obeliscata* ?), 27, 28, 29.

X. *BORAGE* GROUP.

BORAGINACEAE: 30, *Echium*; 31, *Asperugo*.

Ethmia pusiella, Roem.

XI. *CHRYSANTHEMUM* GROUP.

COMPOSITAE (This group can be split into well-defined sub-groups): 32, *Crepis*; 33, *Lactuca*; 34, *Leontodon*; 35, *Sonchus*; 36, *Hieracium*; 37, *Onopordon*; 38, *Cichorium*; 39, *Eupatorium*.

Polia serena, 32, 33, 35, 36, 39; *Cucullia umbratica*, 33, 35, 37, 38; *Polia chrysozona*, 32, 33, 34, 44.

40, *Aster*; 41, *Solidago*; 42, *Senecio*; 43, *Tussilago*.

Cucullia asteris, 40, 41; *Hipocrita jacobaeae*, 42, 43.

44, *Ancistrus*; 45, *Tanacetum*; 46, *Achillea*.

Eupithecia subfulvata, 45, 46; *Eupithecia succenturiata*, 44, 45, 46.

47, *Anthemis*; 48, *Pyrethrum*; 49, *Matricaria*; 50, *Catendula*; 51, *Chrysanthemum*.

Cucullia chamomillae, 47, 48, 49; *Cucullia wredowi*, 47, 50; *Cucullia judaeorum*, 48, 50, 51.

XII. *ERICA* GROUP.

ERICACEAE: 52, *Erica*; 53, *Calluna*.

Anarta myrtilli, *Eupithecia nanata* and *goossensiata*, *Scodiona fagaria*, all on 52 and 53.

XIII. *LAMIUM* GROUP.

LABIATAE: 54, *Lamium*; 55, *Stachys*; 56, *Galeopsis*; 57, *Teucrium*; 58, *Mentha*.

Venilia maculata, 54, 55, 56, 57, 58.

XIV. *CUPRESSUS* GROUP.

CUPRESSACEAE: 59, *Cupressus*; 60, *Juniperus*.

Lithophane lapidea, 59, 60.

XV. *SILENE* GROUP.

CARYOPHYLLACEAE: 61, *Silene*; 62, *Lychnis*; 63, *Dianthus*.

Dianthoecia (*Harmodia*) genus, many sps., 61, 62, 63; *Perizoma flavofasciata*, 61, 62.

XVI. *DELPHINIUM* GROUP.

RANUNCULACEAE: 64, *Delphinium*; 65, *Aconitum*.

Plusia delphini, 64, 65.

XVII. *ASCLEPIAS* GROUP.

ASCLEPIADACEAE: 66, *Asclepias*; 67, *Calotropis*.

Danaus chrysippus, 66, 67.

B. GROUPS ALMOST CORRESPONDING WITH BOTANICAL SYSTEMATIC AFFINITIES.

I. *FRAXINUS* GROUP.

OLEACEAE: 68, *Fraxinus*; 69, *Ligustrum*; 70, *Lonicera*; 71, *Syringa*; 72, *Symphoricarpos*.

Melitaea aurinia, 70, 75; *Haemorrhagia fuciformis*, 70, 72, 74, 75; *Limenitis camilla*, 69, 70; *Lobophora polyommata*, 68, 69, 70; *Hygrochroa syringaria*, 69, 70, 71, 72.

DIPSACEAE: 73, *Dipsacus*; 74, *Knautia*; 75, *Scabiosa*.

(I have excluded from this group, although it has been recorded on most of its species, *Sphinx ligustri*, on the score of its peculiar polyphagy, see Warnecke:—"Ueber die Anpassung der Raupe von *Sphinx ligustri*, L., an fremdlaendische Futterpflanzen" (*Ent. Jahrb.*, 1932).)

II. *ATRIPLEX* GROUP.

CHENOPODIACEAE: 76, *Atriplex*; 77, *Chenopodium*.

POLYGONACEAE : 78, *Rumex*.

Scotogramma trifolii, 76, 77; *Pelurga comitata*, 76, 77, 78; *Eupithecia subnotata*, 76, 77, 78.

III. TYPHA GROUP.

CYPERACEAE : 79, *Scirpus*; 80, *Cladium*.

SPARGANIACEAE : 81, *Sparganium*.

TYPHACEAE : 82, *Typha*.

IRIDACEAE : 83, *Iris*.

Archanara algae (cannae), 79, 82; *Archanara sparganii*, 79, 81, 82, 83; *Plusia festucae*, 81, 83. (This group may have to be excluded as an ecological or biotope group, see below.)

IV. MALVA GROUP.

MALVACEAE : 84, *Malva*; 85, *Lavatera*; 86, *Althaea*; 87, *Gossypium*.

CAESALPINEACEAE : 88, *Ceratonia*.

Earias insulana, 86, 87, 88; *Acontia malvae*, 84, 85, 86; *Acontia graellsii*, 85, 87. (These substitute food-plants have economic importance, their guests being apt to become pests on cotton, 87.)

V. ANGELICA GROUP.

UMBELLIFERAE : 89, *Angelica*; 90, *Cicuta*; 91, *Heracleum*; 92, *Laserpitium*; 93, *Peucedanum*; 94, *Pimpinella*; 95, *Daucus*; 96, *Anethum*; 97, *Carum*; 98, *Torilis*.

CAPRIFOLIACEAE : 99, *Sambucus*.

RUTACEAE : 100, *Ruta*; 101, *Citrus*.

Papilio machaon, 94, 95, 96, 97, 98, 100, 101; *Eupithecia albipunctata*, 89, 90, 91, 92, 93, 94, 99.

VI. BRASSICA GROUP.

CRUCIFERAE : 102, *Brassica*; 103, *Erysimum*; 104, *Raphanus*; 105, *Nasturtium*; 106, *Barbarea*; 107, *Cardamine*; 108, *Sisymbrium*; 109, *Turritis*.

RESEDACEAE : 110, *Reseda*.

Pteris rapae, 102, 103, 104, 105, 110; *Pteris brassicae*, 102, 104; *Euchloë cardamines*, 105, 106, 107, 109; *Lithostege griseata*, 103, 108.

C. GROUPS RUNNING COUNTER TO BOTANICAL SYSTEMATIC AFFINITIES.

I. VITIS-GALIUM GROUP.

AMPELIDACEAE : 111, *Vitis*; 112, *Ampelopsis*.

ONAGRACEAE : 113, *Epilobium*; 114, *Fuchsia*; 115, *Circaea*.

RUBIACEAE : 116, *Galium*; 117, *Rubia*.

Celerio galii, 113, 114, 116, 117; *Hippotion celerio*, 111, 112, 114; *Pergesa elpenor*, 111, 113, 116; *Pergesa porcellus*, 113, 116; *Macroglossum stellatarum*, 116, 117; *Cidaria salicata*, 116, 117; *Cidaria basochesiata*, 116, 117; *Eustroma silaceata*, 113, 115.

II. VIOLA GROUP.

VIOLACEAE : 118, *Viola*.

ROSACEAE : 119, *Fragaria*.

Brenthis euphrosyne, 118, 119

III. QUERCUS-BETULA GROUP.

BETULACEAE : 5, *Betula*.

FAGACEAE : 120, *Quercus*.

Ephyra porata.

IV. QUERCUS-PRUNUS GROUP.

ROSACEAE : 1, *Prunus*.

FAGACEAE : 120, *Quercus*.

Bapta distinctata (pictaria).

(It will be noted that the last three groups, C. II, III, and IV, are erected on the strength of the preferences of a single species only for

each. And perhaps C. IV is incorrect, since I find no other confirmation for Blaschke's record of oak as a food-plant for the "Sloe Carpet Moth." It will also be noted that the species responsible for the systematic diversity of Group C. I are all *Sphingidae*, a systematic group of moths; they appear to display a peculiar intermediate stage of polyphagy and oligophagy.)

It may be asked why the food-plant of *Agrotis ripae* (viz., *Salsola*, *Atriplex*, *Rumex maritimus*, *Cakile*, and *Eryngium maritimum*), which are drawn from four different families, have not been included as a fifth group under C. The reason is that this group of plant species is an ecological group of halophytic character, and that *ripae* is attached to the saline biotope rather than generically to the plants (see, in this connection, Boursin: "Contribution a l'Étude des Agrotidac-Trifinae, xxi": *L'Amateur de Papillons*, 1937 or 1938). The fact that in captivity the larva will thrive on sliced carrot, especially if sprinkled with salt water, is an additional sign that, apart from its halophytic requirements, this larva is basically polyphagous.

Other examples can be given of polyphagous larvae which, by their close attachment to a certain biotope, appear to unite into a preference-group the plants typical of that biotope; we must, in the present context beware of being misled by this appearance, though these cases can be of considerable interest in themselves, and indeed the case of *ripae* is relevant to the "chemotropism" side of this discussion. Six examples of such ecological groups of food-plants are given:—

- (a) Halophytic biotope (see above).
- (b) Moorland biotope (*Salix*, *Vaccinium*, *Erica*, *Calluna*, *Betula*, *Genista*, etc.).
- (c) European woodland biotope (*Quercus*, *Corylus*, *Ulmus*, *Crataegus*, *Prunus*, *Betula*, *Salix*, *Rubus*, etc.).
- (d) Peak biotope (*Astragalus*, *Zygophyllum*, *Silene*, *Rumex*, etc.).
- (e) Marsh biotope (*Carex*, *Cladium*, various *Gramineae*, *Sparganium*, *Phragmites*, *Lysimachia*, *Spiraea*, *Lythrum*, *Inula*). (Group B. III above may come under this heading, and if rightly so should be removed from the table of true preference-groups.)
- (f) Iraqi oasis biotope (*Tamarix*, *Populus*, *Punica*, *Prosopis*, *Zizyphus*, etc.).

Before finally proceeding to consider what light the above table sheds on the main question under discussion, there remain one or two minor incidental remarks to be made, arising out of the review now completed.

The genera *Ulmus*, *Tamarix*, *Rhamnus*, and, with the two exceptions, C. III and IV above, *Quercus*, prove to have no substitute food-plant acceptable to non-polyphagous larvae, though numbers of monophagous larvae are strictly attached to each of them. There are other similar cases of trees and plants with fewer closely attached guest-insects each.

On the main issue, does the evidence of the table support the theory that these preference-groups are primarily due to the associated evolution of plant and insect? (If so, it would not necessarily exclude an explanation in terms of scents and enzymes; for there is much truth in some of Mr Allan's remarks, and indeed I recall having heard tell of

an entomologist breeding a poplar-feeding caterpillar to maturity during the winter in London on cabbage painted with populin-solution!)

In the table, not only do the preference-groups of plants correspond closely, on the whole, to the systematic, i.e. phylogenetic, classification of plants; but the guest-insects show an answering tendency to fall also into groups corresponding to the systematic, i.e. phylogenetic classification of insects.

The latter tendency would be even more apparent had the monophagous larvae not been omitted, among whom examples of systematically closely related larvae feeding on systematically closely related plants are numerous and well-known; it is enough to mention here the *Bryophila* genus (Lichens and Algae), the *Clytie* genus (*Tamarix*) and the *Argynnis* genus (*Viola*). But even in the table the examples of a *Cucullia* group feeding on a *Chrysanthemum* group (A. X.), of a *Dianthoecia* group feeding on a *Silene* group (A. XIV.) and a *Sphingid* group feeding on the *Vitis-Galium* group (C. I.) will probably already have struck the reader as typifying this tendency.

Some species may have been omitted from the table by oversight, but their inclusion would confirm rather than affect the above tendencies revealed by the table.

A tendency of systematically related larvae to have corresponding food-plants also exists in polyphagous species (e.g. *Arctia*, *Agrotis*, etc.).

Mr Donisthorpe's example of the attachment of the *Cionus* beetle-genus to *Verbascum* and *Scrophularia* is quoted by Mr Allan as disproving the theory of "associated evolution of plant and insect" because "beetles preceded . . . flowering plants by some two hundred million years." But does it disprove it?

That beetles in general preceded flowering plants by that period may be so; but it does not necessarily follow that the genus *Cionus* preceded the genera *Verbascum* and *Scrophularia* by that period, unless Coleoptera were fully evolved in their present-day proliferation of species at the end of the Mesozoic Age and underwent no further developments during the Cainozoic. This seems improbable, but is what Mr Allan implies, if his argument is to be taken seriously. The following questions may then be asked about the implied pre-Tertiary history of the genus *Cionus*: To what plants and what ecological routine were they attached? How did they eventually adapt themselves to their present host-plants, so different from their previous hosts, without themselves evolving and changing their identity? What palaeontological evidence is there of this genus preceding the Tertiary Age by "some two hundred million years"? Will some Coleopterist or Palaeontologist give his opinion on the possibility of species and genera of beetle, now attached to flowering-plants, preceding those same plants by "some two hundred million years"?

But even if the possibility is admitted, and the evidence forthcoming, that *Cionus* existed before the origin and evolution of *Verbascum* and *Scrophularia*, does this mean that they have, only a few years ago, become attached to these plants? Can we not, on the contrary, justifiably postulate that they attached themselves to the ancestral type of these plant genera, and maintained the attachment throughout the subsequent evolution of these plants?

Mr Donisthorpe's example, therefore, supports the rest of evidence of the table in favour of the supposition that the associated evolution of plant and insect is the primary cause of the phenomenon of substitute food-plants.

The study of the mechanism whereby inherited organs and instincts operate will, of course, complicate the simple principle of inheritance. But I doubt whether the study of, say, enzymes, has led any biochemist to doubt the theory of evolution, though at times he may become so engrossed in them as not to see the wood for the trees! This, at least, appears to be the case with Mr Allan, and his upper and lower parenchymata.

I conclude by quoting part of a foot-note by Dr Amsel, which appeared in his "Grundsätzliche Bemerkungen zur Frage der Faunenelemente" (Zool. Jahrb. Syst. Oekolog. & Geog. Tiere Abteilung, Band 72, Heft 1/2, Jena, 1939):—"If the larvae of *Xanthospilapteryx syringella*, F., feed on *Syringa*, *Ligustrum*, *Fraxinus*, etc., that is, on plants whose relationship to one another the systematist expresses by including them in one family, the *Oleaceae*, the caterpillars of the above Leaf-mining Moth, prove to us that a true relationship in fact exists. . . . Systematics therefore are not a working hypothesis whose aim is merely the utilitarian aim of bringing order to the study of phenomena, but, on the contrary, their purpose is to recognize and give nomenclatorial expression to actually existing relationships."

Ancestral inheritance is the only reasonable explanation of the characteristics, whether structural or ecological, common to species systematically grouped together.

Food-plant preferences, then, being merely one facet of a species' ecology, have evolved with the rest of the species' peculiarities, and when shared by related species of insect and directed towards related species and genera of plant are a sign of their common associated evolution.

TEPHRITIS SEPARATA, RDI., AN ADDITIONAL BRITISH SPECIES ALLIED TO *T. CONJUNCTA*, LW. (DIPTERA, TRYPETIDAE.)

By J. E. COLLIN, F.R.E.S.

Tephritis conjuncta, Lw., stood in Verrall's *List of British Diptera* under the genus *Euaresta*, Lw., a genus acknowledged by Loew himself to be an artificial group based solely upon the presence of radiating arms from the dark patch near tip of wing. The type of this genus was the N. American *T. festiva*, Lw., which differs from typical species of *Tephritis* not only in having the radial vein with small bristles along its upper (as well as its under) side, but also in having additional "arms" to those present in *conjuncta*, radiating to costa before tip of wing. Our British *conjuncta* agrees with the characters of *Tephritis* and not with this new definition of *Euaresta*, and must remain in the former genus.

In describing *conjuncta* in 1844 Loew especially mentioned the darker femora of the male compared with female and the dark hairs on anterior half of abdominal tergites. He elaborated this description in 1862, including a statement that the black ovipositor of female had pale hairs about base, and for the first time mentioned a variety in which the